Proceedings of the National Shellfisheries Association
Volume 70-1980

INFECTIONS OF *TYLOCEPHALUM* METACESTODES IN COMMERCIAL OYSTERS AND THREE PREDACEOUS GASTROPODS OF THE EASTERN GULF OF MEXICO

Edwin W. Cake, Jr. and R. Winston Menzel

OYSTER BIOLOGY SECTION
GULF COAST RESEARCH LABORATORY
OCEAN SPRINGS, MS 39564

DEPARTMENT OF OCEANOGRAPHY
FLORIDA STATE UNIVERSITY
TALLAHASSEE, FL 32306

ABSTRACT

Acudate glando-procercoids (metacestodes) of Tylocephalum *sp.* sensu *Sparks (1963*b*) (Cestoda; Cephalobothriidae) are reported from the American oyster,* Crassostrea virginica *(Gmelin) (Bivalvia; Ostriedae), and three molluscivorous gastropods in the eastern Gulf of Mexico: the lightning whelk,* Busycon contrarium *(Conrad) (Gastropoda; Melongenidae), the apple murex,* Murex pomum *Gmelin (Muricidae), and the southern oyster drill,* Thais haemastoma canaliculata *(Gray) (Muricidae). Sixty of 138 oysters (43%) from 12 of 17 localities, 79 of 90 whelks (88%) from 14 of 15 localities, 32 of 33 murexes (97%) from 6 of 6 localities, and 23 of 53 drills (43%) from 5 of 8 localities harbored encysted* Tylocephalum *metacestodes. These predaceous gastropods may acquire* Tylocephalum *from oysters and other infected bivalves. No pathological conditions were observed in oysters or their predators.*

INTRODUCTION

Acudate glando-procercoids of one or more unidentified species of *Tylocephalum* (Figure 1) are common parasites of marine mollusks of the eastern Gulf of Mexico and at least two species of *Tylocephalum* occur in molluscivorous, myliobatid stingrays in the Gulf. Cake (1975, 1976, 1978) found metacestodes in 49 of 92 species of Gulf coast mollusks including the American oyster, *Crassostrea virginica*, the lightning whelk, *Busycon contrarium*, the apple murex, *Murex pomum*, and the southern oyster drill, *Thais haemastoma canaliculata*. Burton (1963) described metacestodes of *Tylocephalum* from oysters from Apalachicola Bay, Florida, that had been transplanted into Chincoteague Bay, Virginia, and Quick (1971) reported their presence in oysters at several other localities along the west coast of Florida. Sparks (1963*a*, 1963*b*) and Cheng (1966) reported *Tylocephalum* in *C. virginica* from Hawaii.

Sakaguchi (1973) reported metacestodes of an unidentified species of *Tylocephalum* from four gastropods including two predaceous muricids, *Chicoreus asianus* Kuroda and *Reishia (= Thais) clavigera* (Küster), and from six bivalves including

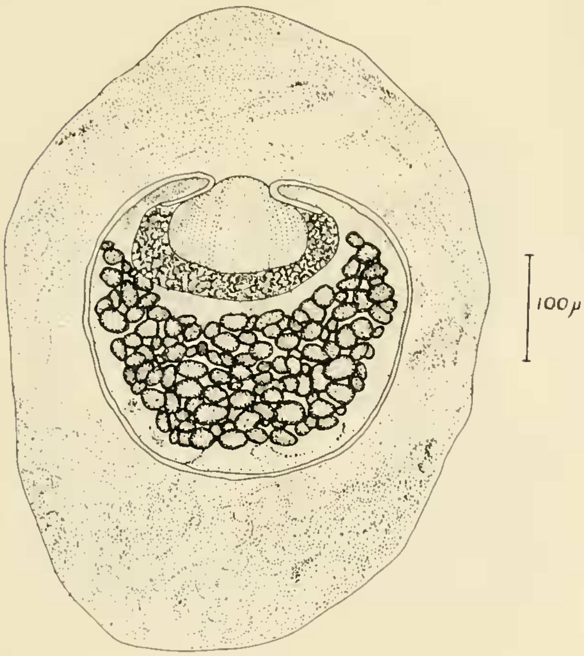

FIGURE 1. *Encysted, acudate glando-procercoid of* Tylocephalum *sp. from the stomach wall of* Crassostrea virginica *(Gmelin).*

the giant Pacific oyster, *Crassostrea gigas* (Thunberg), and the pearl oyster, *Pinctada fucata* (Gould) in Tanabe Bay, Wakayama prefecture, Japan. Sakaguchi "successfully" infected the molluscivorous cat shark ("Nekozame"), *Heterodontus japonicus* (Domeril), with *Tylocephalum* metacestodes from pearl oysters. The metacestodes excysted in the shark's stomach within 24 hours and migrated to the spiral valve within seven days after infection. They remained in the spiral valve but exhibited no maturation during the brief experiment.

Sakaguchi (1973) collected infected oysters and muricid drills from Tanabe Bay, Wakayama prefecture, but did not indicate if they occupied the same habitat. He reported, however, that all of the oysters and muricids examined from that bay were infected with *Tylocephalum* sp.

Tylocephalum metacestodes also infect other edible bivalves and predaceous gastropods. Cake (1976, 1978) found *Tylocephalum* sp. in a total of 33 bivalves (27 "edible") and 16 gastropods (13 predaceous) in the eastern Gulf of Mexico (see also Sakagucki, 1973; and Table 1).

Encysted metacestodes (Figure 1) are generally restricted to the vesicular connective tissue of the digestive gland and the stomach wall of infected mollusks, but infrequently occur in the foot, gills and labial palps of pelecypods, while those in gastropods are generally restricted to the digestive gland (Cake, 1975). Cheng (1966) reported what he believed were infective, ciliated "coracidia" (with penetration glands) intimately associated with gill surfaces and in the stomach of *Tylocephalum*-infected oysters. Wolf (1976) also reported the presence of *Tylocephalum* "coracidia" in the labial palp region of Sydney rock oysters, *Saccostrea (= Crassostrea) commercialis* (Iredale and Roughley), from northern New South Wales and southern Queensland, Australia.

Linton (1916) described adults of *T. marsupium* from the spotted eagle ray, *Aetobatis narinari* (Euphrasen), at Dry Tortugas, Florida, and Tom Mattis (GCRL, Parasitology Section, personal communication) reported adults of *T. pingue* Linton from the cow-nosed ray, *Rhinoptera bonasus* (Mitchill), in East Bay, Panama City, Florida, and from Mississippi Sound. Both of those ray species are well-known mollusk predators (Bigelow and Schroeder, 1953) and *R. bonasus* is a well-known predator of *C. virginica* (Merriner and Smith, 1979).

The predator-prey relationship between the lightning whelk and oysters is well documented (Magelhaes, 1948; Menzel and Nichy, 1958; and Paine, 1962) as is the relationship between the apple murex and oysters (Menzel and Nichy, 1958) and between the southern oyster drill and oysters (Butler, 1953; Chapman, 1958; Menzel et al., 1966; Gunter, 1968; McGraw and Gunter, 1972).

Bivalves and molluscivorous gastropods probably serve as intermediate or paratenic hosts in the life cycle of *Tylocephalum* sp. (Jameson, 1912; Sakaguchi, 1973; Cake, 1975). This report presents infection data that suggest, circumstantially, a transfer of metacestodes from oysters to their predatory gastropods.

The descriptive metacestode term, acudate glando-procercoid, used herein follows the convention of Freeman (1973).

MATERIALS AND METHODS

Oysters and predaceous gastropods were collected from intertidal and shallow, subtidal

TABLE 1. *Synoptic review of bivalve hosts of* Tylocephalum *spp.*

SPECIES	BIVALVE HOST	LOCATION	LOCALITY	REFERENCE
Tylocephalum ludificans Jameson	Pinctada (= *Margaritifera*) *vulgaris* (Schumacher)	Visceral mass, and elsewhere, encysted	Gulf of Mannar and Tricomalee, Sri Lanka (Ceylon)	Herdman & Hornell, 1903 Southwell, 1924 Willey, 1909
T. margaritifera Seurat	*P.* (= *M.*) *margaritifera cumingi* (Reeve)	Throughout body, encysted	Gambier Islands	Seurat, 1906
T. minus Jameson	*P. vulgaris*	Throughout body, encysted	Gulf of Mannar, Sri Lanka (Ceylon)	Shipley & Hornell, 1904
Tylocephalum sp.	*Arca rhombea* Born	Digestive gland, encysted	Sambore River, Sri Lanka (Ceylon)	Willey, 1907
Tylocephalum sp.	*Argopecten* (= *Aequipecten*) *irradians* (Say)	Stomach walls and gills, encysted	Beaufort, North Carolina	Gutsell, 1930
Tylocephalum sp.	*Chamys nobilis* (Reeve)	Digestive gland, encysted	Tanabe Bay, Wakayama pref., Japan	Sakaguchi, 1973
Tylocephalum sp.	*Crassostrea gigas* (Thunberg)	Gills, encysted	Coasts of Hong Kong and Peoples' Republic of China	Cheng, 1975
Tyocephalum sp.	*C. gigas*	Digestive gland, encysted	Tanabe Bay, Wakayama pref., Japan	Sakaguchi, 1973
Tylocephalum sp.	*C. madrasensis* (Preston)	Gills, encysted	Mulki, State of Karnataka, India	Stephen, 1978
Tylocephalum sp.	*C. virginica* (Gmelin)	(Unknown)	(Unknown)	Tennet, 1906

TABLE 1. *Continued*

Tylocephalum sp.	*C. virginica*	Gills, gut epithelium, palps, encysted	Apalachicola Bay, Florida	Burton, 1963
Tylocephalum sp.	*C. Virginica*	Digestive diverticula, encysted	West Loch, Pearl Harbor, Hawaii	Sparks, 1963 *a, b*
Tylocephalum sp.	*C. virginica*	Gills and stomach (coracidia); gut wall, digestive gland, encysted	West Loch, Pearl Harbor, Hawaii	Cheng, 1966
Tylocephalum sp.	*C. virginica*	Connective, leydig tissues, encysted	Choctawhatchee and Tampa Bays, Florida	Quick, 1971
Tylocephalum sp.	*C. virginica.*	(Unknown)	Coasts of Georgia and North Carolina	Sindermann and Rosenfield, 1968
Tylocephalum sp. (= *Monobothrium)*	*Meleagrina occa* Reeve & *M. irradians* Reeve	Digestive gland	Nossi-Be, Madagascar	Seurat, 1906
Tylocephalum sp.	*Mytilus edulis* Linné	Digestive gland, encysted	Tanabe Bay, Wakayama pref., Japan	Sakaguchi, 1973
Tyocephalum sp.	*Placuna placenta* Linné	Digestive gland, encysted	Lake Tampalakaman, Tuticorin, Sri Lanka (Ceylon)	Hornell, 1905
Tylocephalum sp.	*P. placenta*	Digestive gland, encysted	Sambore River and Lake Tamblegam, Sri Lanka (Ceylon)	Willey, 1907
Tylocephalum sp.	*Pinctada fucata* (Gould)	Digestive gland, encysted	Tanabe Bay, Wakayama pref., Ago Bay, Mie pref., Japan	Sakaguchi, 1973
Tylocephalum sp.	*P. vulgaris*	(Unknown)	Eniwetok Atoll	Cheng & Rifkin, 1970

TABLE 1. *Continued*

Tylocephalum sp.	*Pinna bicolor* Gmelin (= *P. attenuata* Reeve)	Digestive gland, encysted	Tanabe Bay, Wakayama pref., Japan	Sakaguchi, 1973
Tylocephalum sp.	*Saccostrea* (= *Crassostrea*) *commercalis* (Iredale & Roughley)	Gills and palps, (coracidia); digestive gland, encysted	Northern New South Wales & southern Queensland, Australia	Wolf, 1976
Tylocephalum sp.	*S.* (= *C.*) *echinata* (Quoy & Gaimard)	Digestive diverticula, encysted	Northern Territory, Australia	Wolf, 1976
Tylocephalum sp.	*Spondylus barbatus* Reeve	Digestive gland, encysted	Tanabe Bay, Wakayama pref., Japan	Sakaguchi, 1973
Tylocephalum sp.	*Tapes philippinarum* (= *T. semidescusata*) (Adams & Reeve)	Digestive diverticula, encysted	Kaneohe Bay, Oahu, Hawaii	Cheng & Rifkin, 1968
Tylocephalum sp.	*Venus* spp.	Digestive gland, encysted	Sambore River, Sri Lanka (Ceylon)	Willey, 1907

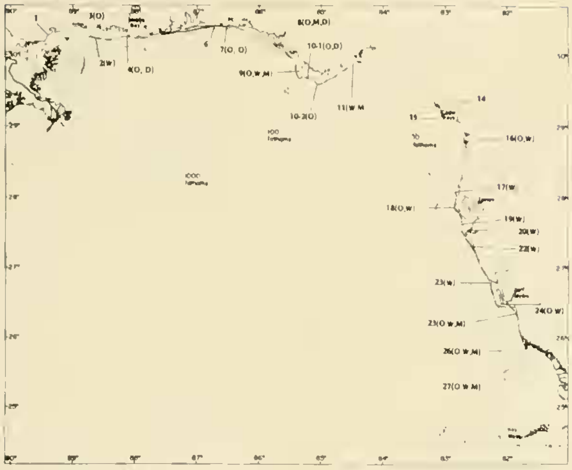

FIGURE 2. *Gulf of Mexico localities where* Tylocephalum *metacestodes occurred in oysters (O), lightning whelks (W), apple murexes (M), and oyster drills (D).*

habitats at 24 localities between St. Louis Bay, Mississippi, and the Ten Thousand Islands of south Florida (Figure 2), and maintained alive in Styrofoam® tanks of aerated seawater until examined. During necropsy the following tissues and locations were examined with the aid of a dissecting microscope: (in oysters) gills, labial palps, stomach and stomach wall, and digestive diverticula; (in gastropods) lumen of stomach and digestive gland (exterior).

Accurate quantification of infection intensities (number of metacestodes per host) in oysters and predaceous gastropods was not practical during this investigation. Because of the small size of the *Tylocephalum* metacestodes (length, 144 to 340 μ) and the nature of the digestive gland tissues, exact counts would have required serial sectioning and light microscopic examination of those tissues and locations where metacestodes would occur if the mollusk was infected. Intensities were based, therefore, on the examination of fresh tissues and we believe that the infection data reported herein are valid for comparison of the four hosts under consideration.

RESULTS

Infected oysters occurred at 12 of 17 localities throughout the eastern Gulf of Mexico, where 60 of 138 oysters (44%) contained an average of 15.8 metacestodes. Infected lightning whelks occurred at 14 of 15 localities, all but two of which were east of the Apalachicola River, where 79 of 90 whelks (88%) contained an average of 10.3 metacestodes. Infected apple murexes occurred at 6 of 6 localities, three each in the northeastern and southeastern Gulf, where 32 of 33 murexes (97%) contained an average of 22.1 metacestodes. Infected oyster drills occurred at 5 of 8 localities, all but one of which were west of the Apalachicola River, where 23 of 53 drills (43%) contained an average of 14.0 metacestodes. The infection data are summarized in Table 2.

Oysters and drills were collected from the same oyster reef habitat at four localities west of the Apalachicola River (Stations 4, 6, 7 and 10-1; Figure 2). Both species were infected with *Tylocephalum* at Station 4, 6 and 10-1; neither were infected at Station 7. Infected oysters and whelks were collected from the same reef habitat at Station 18. Infected oysters, whelks, and murexes were collected from the same reef habitat at four localities in southern Florida (Stations 24, 25, 26 and 27).

The relative incidence (percent infected) and intensity (number per host) of infections of *Tylocephalum* in oysters and predaceous gastropods were similar at most stations, especially where the mollusks occurred together in the same reef habitat. At those localities where oysters were uninfected, but whelks were infected (Stations 22 and 23), the two species did not occupy the same habitat. The whelks were foraging on other bivalves, many of which were infected with *Tylocephalum* sp. (Cake, 1976).

Of the three gastropods, *Murex pomum* exhibited the highest infection incidence (97%) and intensity (22.1 metacestodes per murex). The infection incidences and intensities for oysters and drills were similar (44 vs. 43% and 15.8 vs. 14.0 metacestodes per mollusk, respectively) but the data base was limited. All predatory gastropods examined were infected at six localities where they were foraging on infected oysters (Stations 10-1, 18, 24, 25, 26, and 27).

All infected mollusks appeared to be otherwise healthy (i.e., none were weak or moribund, or exhibited significant loss of body volume and weight). In no case was the digestive tract blocked by massive infections as was observed by one of us (EWC) in the case of encysted plerocercoids of

TABLE 2. *Infection data summary from four molluscan hosts of* Tylocephalum *sp.* (sensu *sparks) in the eastern Gulf of Mexico.*

STA NO	LOCALITIES	*CRASSOSTREA VIRGINICA*	*BUSYCON CONTRARIUM*	*MUREX POMUM*	*THAIS HAEMASTOMA CANALICULATA*	REMARKS
1	Bay St. Louis, MS	0/10				
2	Horn Island, MS		2/5; 15*			
3	Deer Island & Davis Bayou, MS	1/15; 1				
4	Dauphin Island, AL	1/15; 1			4/4; 65	*C.& T.* together
6	Santa Rosa Sound, Navarre, FL	0/10			0/5	*C. & T.* together
7	Choctawhatchee Bay, Destin, FL	10/10; 128			4/10; 34	*C. & T.* together
8	Grand Lagoon, St. Andrew Bay (entrance), FL	10/10; 32		10/10; 97	2/10; 4	
9	Eagle Harbor & Black's Island, St. Joseph Bay, FL	5/10; 18	5/6; 22	4/5;7		
10-1	Indian Lagoon, Apalachicola Bay, FL	10/10; 570			10/10; 163	*C.& T.* together
10-2	Cape St. George, FL				3/3; 55	
11	Alligator Harbor & St. Teresa Beach, FL		20/23; 108	3/3; 115	0/10	
14	Suwannee River (entrance), FL	0/3				
15	Seahorse Key, Cedar Key, FL		0/1			
16	Crystal River (power plant canals), FL	2/5; 5	2/3; 4		0/1	
17	North Anclote Key, FL		5/6; 45			
18	Clearwater (Pass), FL	4/6; 14	3/3; 15			*C. & B.* together
19	Mullet and Mandelaine Keys, Boca Cicga Bay, FL		3/3; 75			
20	Snead Island, Tampa Bay, FL		1/1; 1			
22	Big Sarasota (Bay) Pass, FL	0/5	2/3; 35			

TABLE 2. *Continued*

23	Gasparilla Sound, Placida, FL	0/5	4/4, 60			
24	York Island, Pine Island Sound, FL	3/5; 3	10/10; 97			*C.* & *B.* together
25	Estero Bay & Big Carlos Pass, FL	3/5; 55	7/7; 135	10/10; 410		*C.*, *B.* & *M* together
26	Cape Romano Shoals, FL	3/4; 57	10/10; 110	2/2; 30		*C.*, *B.* & *M.* together
27	Indian Key & Chokoloskee Bay (Everglades City), FL	8/10; 66	5/5; 90	3/3; 47		*C.*, *B.* & *M.* together
	TOTALS	60/138; 950*	79/90; 812*	32/33; 706*	23/53; 321*	
	INCIDENCE OF INFECTION (%)	43.5	87.8	97.0	43.4	
	MEAN INFECTION INTENSITY (# / Infected Host)	15.8	10.3	22.1	14.0	
	MAXIMUM INFECTION INTENSITY	125+	25+	75+	50+	
	MOLLUSK SIZE RANGE (mm)	50-110	73-290	43-80	40-70	

* [# Infected Hosts / # Mollusks Examined (at that station); # *Metacestodes*]

Parachristianella sp. *sensu* Cake (1976) which completely blocked the intestine of a heavily infected sunray venus clam, *Macrocallista nimbosa* (Lightfoot).

DISCUSSION

We believe that predaceous gastropods become infected with metacestodes of *Tylocephalum* by ingesting infected oyster tissues. We are unaware of any biochemical, physical, or physiological factors that would prevent the transfer of infective metacestodes from oysters to gastropods during feeding. The metacestodes are small enough to be ingested without destruction during the rasping of the gastropod's radula. The gastropod's gut environment is probably suitable physiologically for at least a short time since tetraphyllidean plerocercoids are common gut parasites of molluscivorous gastropods in the Gulf of Mexico (including *B. contrarium, M. pomum,* and *T.h. canaliculata*) (Wardle, 1974; Cake, 1976). Once liberated from the oyster tissues in the gastropod gut, the metacestodes could migrate to other regions including the digestive gland via the diverticula. Since the cyst that surrounds the metacestodes in both the oyster and the gastropod is of host-origin, the metacestodes are probably subject to re-encystment in the gastropod host. The presence of metacestodes in the digestive gland of the gastropod, instead of in the lumen of the gut (or gut epithelium as in the oyster), indicates definite site-selection in the gastropod; however, Wardle (1974) found similar metacestodes free in the gut of *T. haemastoma* (= *T.h. canaliculata*). The presence of metacestodes in the digestive tract of predaceous gastropods also suggests that the infection occurred during feeding rather than from a penetration of the external surface by the metacestodes or earlier infective stages.

Cheng (1966) and Wolf (1976) observed small, ciliated, multicellular organisms in the gut and associated with the gills of oysters that were infected with encysted metacestodes of *Tylocephalum.* They concluded that the organisms were "coracidia" (free-swimming stages which hatch from aquatic cestode eggs and which are precursors of metacestodes). The possibility that the infected gastropods in this investigation acquired infections of *Tylocephalum* via gill-penetration of "coracidia" as suggested by Cheng (1966) was not considered plausible primarily because no coracidial stage has yet been demonstrated in the ontogeny of any known lecanicephalidean cestode. Cheng's "coracidia" were five to seven times larger than those known from species of marine pseudophyllidean and tetrarhynchidean cestodes. Cheng's "coracidia" also lacked the larval hooks that are typical of the coracidia of other marine cestodes, and the ciliated epithelium illustrated by Cheng appears to be part of an epidermis rather than a ciliated embryophore that surrounds the oncosphere of a true coracidium (Rybicka, 1966). Cheng's observations notwithstanding, no penetration glands have been observed in marine coracidia (Rybicka, 1966; Tom Mattis, GCRL Parasitology Section, personal communication). Cheng's "coracidia" are probably not the precursors of the metacestodes of *Tylocephalum,* but are perhaps advanced metazoan larvae of another oyster symbiont.

If no coracidium exists in the ontogeny of *Tylocephalum,* filter-feeding mollusks such as *C. virginica* may become infected by ingesting planktonic or demersal eggs that contain oncospheres. We cannot, however, entirely eliminate the possibility that oysters may ingest the remains of small, infected, first intermediate hosts such as copepods. That pathway appears unlikely, however, since oysters "select" food particles within the size range of approximately 1 to 10 μ. The smallest eggs of most marine cestodes are somewhat larger than 10 μ but may be ingested infrequently. The physical action of the oyster's gastric mill and the biochemical action of the gut enzymes may permit the oncosphere to escape from the egg and penetrate the stomach wall. The ingested-egg pathway may also account for the *Tylocephalum* infections that Cake (1976) observed in three species of filter-feeding gastropods of the genus *Crepidula* in the eastern Gulf of Mexico.

ACKNOWLEDGEMENTS

We wish to thank the Florida State University Departments of Biological Sciences and Oceanography and James Byram (Peter Bent Brigham Hospital, Pathology Department, Boston, Mass., formerly with the FSU Dept. Biol. Sci.) for financial, logistical, and technical assistance. Tom Mattis, GCRL, kindly shared his extensive knowledge of cestodes of the northeastern Gulf of Mexico and Byram and Mattis critically reviewed the manuscript. The Gulf Coast Research Laboratory provided support and assistance to one of us during the preparation of the manuscript.

LITERATURE CITED

Bigelow, H.B., and W.C. Schroeder. 1953. Fishes of the western North Atlantic: II. Sawfishes, guitarfishes, skates and rays. Mem. Sears. Found. Mar. Res. (Yale Univ., New Haven, Conn.); no. 1:1-514.

Burton, R.W. 1963. Report on a cestode microparasite of the oyster, *Crassostrea virginica*, in Florida. Shellfish Mortality Conference. Jan. 29-30, 1963. Oxford, Maryland. 6 p. (Mimeo.)

Butler, P.A. 1953. The southern oyster drill. Proc. Natl. Shellfish. Assoc. 44:67-75.

Cake, E.W., Jr. 1975. Larval and postlarval cestode parasites of shallow-water, benthic mollusks of the Gulf of Mexico from the Florida Keys to the Mississippi Sound. Tallahassee, FL: Florida State University. Available from: University Microfilms, Ann Arbor, MI; Publ. no. 75-15,488. 434 p. Dissertation. (Diss. Abstr. 36:40-41B).

Cake, E.W., Jr. 1976. A key to larval cestodes of shallow-water, benthic mollusks of the northern Gulf of Mexico. Helminthol. Soc. Wash., Proc. 43(2):160-171.

Cake, E.W., Jr. 1978. Larval cestode parasites of edible mollusks of the northeastern Gulf of Mexico. Gulf Res. Repts. 6(1):1-8.

Chapman, C.R. 1958. Oyster drill *(Thais haemastoma)* predation in Mississippi. Proc. Natl. Shellfish. Assoc. 49:87-97.

Cheng, T.C. 1966. The coracidium of the cestode *Tylocephalum* and the migration and fate of this parasite in the American oyster, *Crassostrea virginica*. Trans. Amer. Microscop. Soc. 85:246-255.

Cheng, T.C. 1975. New geographic records for *Tylocephalum* metacestodes. J. Invertebr. Pathol. 26:395-396.

Cheng, T.C., and E. Rifkin. 1968. The occurrence and resorption of *Tylocephalum* in the clam, *Tapes semidecussata*. J. Invertebr. Pathol. 10:65-69.

Cheng, T.C., and E. Rifkin, 1970. Cellular reactions in marine molluscs in response to helminth parasitism. Snieszko, S.F., ed. A symposium on diseases of fish and shellfishes. Washington, D.C.: Amer. Fish. Soc. Spec. Publ. no. 5:443-496.

Freeman, R.S. 1973. Ontogeny of cestodes and its bearing on their phylogeny and systematics. In: Advances in Parasitology, B. Dawes, ed. Academic Press, N.Y. vol. 11:481-557.

Gunter, G. 1968. Some factors concerning the drilling apparatus and the feeding and predation of prosobranchiate gastropods especially on other molluscs. Proceedings of Symposium on Mollusca. Mar. Biol. Assoc. India. I:370-378.

Gutsell, J.S. 1930. Natural history of the bay scallop. Bull. U.S. Bureau Fish. 46:569-631.

Herdman, W.A. and J. Hornell. 1903. Note on pearl-formation in the Ceylon pearl oyster. British Assoc. Rept., Southport. 695 p.

Hornell, J. 1905. Report on the *Placuna placenta* pearl fishery of Lake Tampalakaman. Ceylon Sessional Papers. 14 p.

Jameson, H.L. 1912. Studies on pearl-oysters and pearls. I. The structure of the shell and pearls of the Ceylon pearl-oyster *(Margaritifera vulgaris* Schumacher): with an examination of the cestode theory of pearl production. Zool. Soc. London, Proc. 11:260-358.

Linton, E. 1916. Notes on two cestodes from the spotted sting ray. J. Parasitol. 3:34-38.

Magelhaes, H. 1948. An ecological study of snails on the genus *Busycon* at Beaufort, North Carolina. Ecol. Monogr. 18:377-409.

McGraw, K.A., and G. Gunter. 1972. Observations on killing of the Virginia oyster by the Gulf oyster borer, *Thais haemastoma*, with evidence for a paralytic secretion. Proc. Natl. Shellfish. Assoc. 62:95-97.

Menzel, R.W., and F.E. Nichy. 1958. Studies on the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. Bull. Mar. Sci. Gulf Carib. 8(2):125-145.

Menzel, R.W., N.C. Hulings, and R.R. Hathaway. 1966. Oyster abundance in Apalachicola Bay, Florida, in relation to biotic associations influenced by salinity and other factors. Gulf Res. Repts. 2(2):73-96.

Merriner, J.V., and J.W. Smith. 1979. A report to the oyster industry of Virginia on the biology and management of the cownose ray (*Rhinoptera bonasus* Mitchill) in lower Chesapeake Bay. Va. Inst. Mar. Sci. Spec. Rept. Applied Mar. Sci. and Ocean Engin. no. 216:33 p.

Paine, R.T. 1962. Ecological diversification in sympatric gastropods of the genus *Busycon*. Evolution 16:515-523.

Quick, J.A., Jr. 1971. Pathological and parasitological effects of elevated temperatures on oysters with emphasis on *Labyrinthomyxa marina*. In: A preliminary investigation: the effect of elevated temperatures of the American oyster, *Crassostrea virginica* (Gmelin), J.A. Quick, ed. Fla. Dept. Nat. Res. Prof. Paper Ser. no. 15:105-171.

Rybicka, Krystyna. 1966. Embryogenesis in cestodes. In: Advances in parasitology, B. Dawes, ed. Academic Press, N.Y. vol. 4:107-186.

Sakaguchi, 1973. A larval tapeworm, *Tylocephalum*, in marine molluscan shellfishes. Bull. Nansei Reg. Fish. Res. Lab. 6:1-9.

Seurat, L.G. 1906. Sur un cestode parasite des huîtres déterminant la production des perles fines aux îles Gambier. C.R. Hebd. Séanc. Acad. Sci., Paris 142:801-803.

Shipley, A.E., and J. Hornell. 1904. The parasites of the pearl oyster. Herdman, W.A., ed. Report to the Government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar. Royal Soc. Lond. part 2:77-106.

Sindermann, C.J., and A. Rosenfield. 1968. Principal diseases of commercially important marine bivalve Mollusca and Crustacea. Fish. Bull. 66(2):335-385.

Southwell, T. 1924. The pearl-inducing worm in the Ceylon pearl oyster. Ann. Trop. Med. Parasitol. 18:37-53.

Sparks, A.K. 1963*a*. Survey of the oyster potential of Hawaii. Hawaii Div. Fish and Game. 44 p.

Sparks, A.K. 1963*b*. Infection of *Crassostrea virginica* (Gmelin) from Hawaii with a larval tapeworm, *Tylocephalum*. J. Insect Pathol. 5(3):284-288.

Stephen, D. 1978. First record of the larval cestode *Tylocephalum* from the Indian backwater oyster, *Crassostrea madrasensis*. J. Invertebr. Pathol. 32:110-111.

Tennent, D.H. 1906. A study of the life-history of *Bucephalus haimeanus*, a parasite of the oyster. Quart. J. Microscop. Sci. N.S. 49(4):635-690.

Wardle, W.J. 1974. A survey of the occurrence, distribution and incidence of infection of helminth parasites of marine and estuarine Mollusca from Galveston, Texas. College Station, TX, Texas A&M University. Available from: University Microfilms, Ann Arbor, MI; Publ. no. 74-21,235. 346 p. Dissertation. [Diss. Abstr. 35(4B):1516.]

Willey, A. 1907. Report on the window-pane oyster (*Placuna placenta*, "Muttuchchippi") in the backwaters of eastern province (June 1907). Spolia Zeylanica 5(17):33-56.

Willey, A. 1909. Report of the marine biologist for 1908. Ceylon Administration Reports for 1908, Colombo, p. G. 1.

Wolf, P.H. 1976. Occurrence of larval stages of *Tylocephalum* (Cestoda: Lecanicephaloidea) in two oyster species from Northern Australia. J. Invertebr. Pathol. 27:129-131.